

5.—The *Amphibolurus maculatus* species-group (*Lacertilia*, *Agamidae*) in Western Australia

By G. M. Storr*

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The "species" *Amphibolurus maculatus* of authors consists in Western Australia of ten taxa: *A. femoralis* sp. nov., *A. fordii* sp. nov., *A. m. badius* subsp. nov., *A. m. maculatus* (Gray) *A. m. griseus* subsp. nov., *A. m. dualis* subsp. nov., *A. i. rubens* subsp. nov., *A. i. isolepis* (Fischer), *A. i. gularis* Sternfeld and *A. i. citrinus* subsp. nov. Length of appendages relative to trunk varies with age, sex and latitude. Some, if not all, of these lizards live only for one year. Their habitat preferences and phylogeny are discussed.

Introduction

Until recently this section of the genus *Amphibolurus* presented no difficulties. With the limited series available to them, Loveridge (1934) and Glauert (1961) believed that it only consisted of the species *maculatus* Gray, the nominate race occurring in south-western Australia, and the race *gularis* Sternfeld from further north and east.

Much material has been collected in the last few years, and the simple concepts of earlier workers have had to be abandoned. First it became evident that in certain areas *gularis* and *maculatus* were sympatric, which required their recognition as full species, each, as it happened, divisible into four races. Moreover, another two species were discovered. Thus, instead of one species and one subspecies, there are now known from Western Australia four species and at least six subspecies.

Except for specimens kindly lent by Messrs. A. Kluge and D. Bradshaw, all material examined is lodged in the Western Australian Museum. Unless stated to the contrary, all localities are in this State.

Amphibolurus maculatus Group

Diagnosis

This group consists of small to medium-sized, active, non-burrowing, non-climbing agamids in which the homogeneous dorsal scales are strongly uncarinate, the alignment of the keels converging back towards the midline. There are no nuchal and dorsal crests. There is little or no development of clumps of tubercles behind the gape and on the side of neck.

Additional characters shared by all taxa

Head, body and base of tail moderately depressed. Tail long and tapering gradually. Supraciliary ridge acute. Rostral ridge moderately acute and entirely superior to fairly large nasal shield. Nostril a little nearer to orbit than tip of snout. Rostral and mental distinctly larger than labials, which are scarcely different in size and shape from the scales above and below them. Scales on top of head moderately large and rugosely uncarinate. Scales on neck very much smaller than those on head and back. Scales on back and upper surface of limbs and tail strongly imbricate and keeled. Scales on sides of body smooth or weakly keeled and much smaller than dorsals and ventrals. Preanal and

femoral pores well developed in males, but often indiscernible in females. Toes long and slender with 24-37 lamellae under the fourth. Claws long and sharp. Adult and subadult males marked below with characteristic black pattern.

Differentiation of Species

The four species are distinguished mainly on dorsal coloration and pattern, the extent and shape of the ventral markings in males, the extent of the femoral pores, the alignment and continuity of the preanal pores, the degree of lateral compression of toes, and the nature of subdigital carination. Because the best characters are confined to or easily ascertained only in adult males, the identification of females and juveniles may prove difficult.

Many females, perhaps most, will be recognisable by some development of the characters that are species-specific for males. In any case they will be closely associated with males of their own species and will seldom be collected without them. With juveniles, coloration and pattern should be compared with those of adults from the same area (either directly or by reference to the descriptions herein), and a careful search should be made for pores under medium-power microscope. When pores are not evident their future extent and alignment can be guessed at by locating the sharp boundary between the large anteroventral scales of the thigh and the small posteroventral scales.

Distribution

The *maculatus* species-group is restricted to the more arid parts of Australia, and is especially found in sandy country with low, open vegetation. The four species in Western Australia collectively range throughout the State except the extreme north and south-west.

Key to species (based on male characters)

1. Pores more than 32 and extending more than half-way down thigh; throat marked with black 2
Pores fewer than 33 and extending only to middle of thigh; no black on throat *femoralis*
2. Alignment of preanal pores strongly arched forwards; gular markings solid black; post-gular markings extend at least to anterior part of abdomen *isolepis*
Alignment of preanal pores not strongly arched forwards; gular markings not solid black; post-gular markings confined to chest 3
3. Pores more than 36 and extending to knee; a black chevron on throat *maculatus*
Pores fewer than 43, not extending on to distal quarter of thigh; throat spotted with black *fordii*

*Western Australian Museum, Perth, Western Australia.

***Amphibolurus maculatus badius* subsp. nov.**

Holotype.—R 18624 (in Western Australian Museum), an adult male collected by G. M. Storr and B. T. Clay on October 31, 1961.

Type locality.—15 miles south-east of Cardabia, Western Australia, in lat. 23° 15' S and long. 113° 55' E.

Paratypes.—R 18618 (18 mi. SSW of Bullara); R 16986-90, R 18605-10 (Ningaloo); R 16985 (7 mi. SE of Ningaloo); R 16872, R 16983, R 18611-7 (12 mi. SSE of Ningaloo); R 16875, R 16879 (15 mi. SSE of Ningaloo); R 16973-4 (14 mi. N of Cardabia); R 16969-70 (11 mi. N of Cardabia); R 16968 (8 mi. N of Cardabia); R 18619-23 (4 mi. N of Cardabia); R 16955-65 (3 mi. SE of Cardabia); R 18625 (11 mi. SE of Cardabia); R 18626-8 (4 mi. S of Gnaraloo); R 18629-35 (18 mi. N of Quobba); R 18637-41 (Quobba); R 17317, R 18642-3 (6 mi. S of Quobba); R 18644-56 (24 mi. N of Carnarvon).

Diagnosis.—The small size and reddish coloration distinguish *badius* from all other races of *maculatus*.

Description.—Head and tail brown; back reddish brown to brick-red. Yellow dorsolateral stripe from neck to rump, either continuous or broken by short, dark brown, transverse bars constricted in middle (where they cross dorsolateral stripe) and thus shaped like hourglass. These bars contract on tail into spots which coalesce to form dark dorsolateral stripe of irregular width. Immediately below these dark bars and spots a pale lateral stripe. Edge of lower jaw bright yellow. Remainder of under-surface whitish, except for following black or dark grey markings in male: chevron-shaped mark on throat, and bar across chest which is broken or constricted at midline.

Upper labials 10-14. Line of 41-57 pores extending almost to knee, continuous or slightly broken at midline and bowed slightly forwards. Gulars and ventrals keeled. Toes compressed, denticulate along outer edge of their upper surface. Lamellae under fourth toe 24-31, V-shaped in section and spinosely bicarinate, the inner series of keels apical and much the larger, the outer series lateral and often indiscernible except on distal phalanx. Maximum snout-vent length: males 52, females 54.

Distribution.—Mid-west coast of Western Australia from Ningaloo south to Carnarvon, thence east and south-east to Doorawarra and Narryer.

Comments.—North of the Gascoyne River, suitable habitat for this race is practically continuous in coastal dunes and near-coastal sandplains. Here the lizards are not only very numerous, but also undergo little geographical variation.

The coastal country from the Gascoyne to the Wooramel River is low-lying and consists largely of mangrove and samphire swamps; inland from these are plains of heavy soil, equally unsuitable for *A. maculatus*. The species is thus restricted in this region to isolated ridges of red sandy loam. The scattered populations on these ridges differ slightly and variously from typical *badius*. Though tentatively placed with *badius*, specimens from 23 miles SSE of Carnarvon, 9 miles W of Doorawarra, and from

Narryer, have not been used for descriptive purposes.

***Amphibolurus maculatus maculatus* (Gray)**

Uromastix maculatus J. E. Gray, 1831, a synopsis of the species of the Class Reptilia, p. 62, in Griffith's "Animal Kingdom" 9.

Grammatophora gaimardi Duméril & Bibron, 1837, "Erpétologie générale" 4: 470. Near Shark Bay (Quoy & Gaimard).

Material examined.—R 13153-9, R 20465-93 (Bernier Island); R 13146-52 (Dorre Island); R 12771 (Gregory, Peron Peninsula); Bradshaw collection (6 mi. S of Denham); R 13291 (8 mi. N of Galena); R 13139 (33 mi. E of Ajana); R 18592 (20 mi. SE of Kalbarri); R 11358 (5 mi. E of Kalbarri); R 16929-35 (14 mi. S of Kalbarri); R 18659-60 (Port Gregory); R 18661 (4 mi. S of Geraldton); R 22256-63 (Cliff Point); R 13411 (Stockyard Gully); R 12210, R 12689-91 (Jurien Bay); R 13441-2, R 18662 (lower Hill River).

Diagnosis.—Larger and duller than *maculatus badius*; smaller and browner than *maculatus griseus* and having relatively longer appendages.

Description.—Dorsally dull brown, with or without fine black spots. Creamy to brownish yellow dorsolateral stripe from neck to rump, continuous or broken by short transverse bars constricted in their middle by dorsolateral stripe and thus shaped like hourglass or dumb-bell. Above and below dorsolateral stripe a series of small pale spots alternating with dark transverse bars. Lower half of transverse bars coalesce on tail to form continuous dorsolateral stripe of irregular width. Pale grey lateral stripe from neck, over insertion of arm, to groin where it continues down inner edge of thigh; it reappears on outer edge of thigh and extends back to proximal half of tail. Dark ventrolateral stripe from axilla, back along flanks and both sides of thigh, to base of tail. Underneath whitish except for following black markings in males: small patch on chin, spots on lower lips, chevron on throat (bowed outwards and thickest anteriorly), and rhombic or kite-shaped patch on chest.

Upper labials 10-15. Line of 40-53 pores extending almost to knee, continuous or broken and slightly or moderately bowed forwards at midline. Gulars and ventrals keeled. Toes slightly compressed and moderately denticulate along outer edge of upper surface. Lamellae under fourth toe 25-37, V-shaped in section, sharply bicarinate, the inner series of keels apical, the outer series lateral and much the smaller. Maximum snout-vent length: males 58, females 59.

Distribution.—Coastal dunes and near-coastal sandplains of Western Australia from Shark Bay (Bernier and Dorre Islands and Peron Peninsula) south to the lower Hill River.

Comments.—In his original description of *maculatus* in 1831, Gray gave no details of the provenance of his type, except to indicate that it was in the Paris Museum. It was almost certainly the unique specimen on which Duméril & Bibron based *gaimardi* in 1837. At any rate these authors declared the two to be synonymous, and Gray's redescription of *maculatus* in 1845 is obviously adapted from Duméril & Bibron's excellent account of *gaimardi*.

The precise locality of the type of *gaimardi* is unknown. Quoy & Gaimard, during their visit to Shark Bay on the *Uranie* in 1818, made general collections on Dirk Hartogs Island and Peron Peninsula. I know of no material of *maculatus* from Dirk Hartogs Island.

***Amphibolurus maculatus griseus* subsp. nov.**

Holotype.—R 21708 (in Western Australian Museum), an adult male collected by G. M. Storr on November 11, 1963.

Type locality.—14 miles west of Boorabbin, Western Australia, in lat. 31° 15' S and long. 120° 05' E.

Paratypes.—R. 13140 (8 mi W of Coorow), R 14021 (10 mi. S of Coorow), R 5740 (Manning), R 12296 (Dumbleyung), R 6074 (Kuerin), R 12616 (Tarin Rock), R 2520-3 (Ongerup), R 21742-4 (Lake Magenta Reserve), R 10482 (Ravensthorpe district), R 21530 (Holt Rock), R 21709 (14 mi. W of Boorabbin).

Diagnosis.—Distinguished from nominate *maculatus* by its large size, much shorter tail, greyer coloration, and broad reddish dorsolateral stripe.

Description.—Dorsally grey or brownish grey. Broad orange-red dorsolateral stripe from neck to rump, sometimes continuous but usually broken by black or dark brown transverse bars shaped like dumb-bells. Lower half of these bars extend on to tail as a more or less continuous line of spots, and upper half extend forward, almost to eye, as a crooked black line. Broad greyish white lateral stripe from side of neck, over insertion of arm and along flanks, to groin where it continues along inner edge of thigh, reappearing on outer edge and extending back to proximal half of tail where it is usually whiter than on flanks. Broad, more or less broken, black or dark brown ventrolateral stripe from axilla, back along flanks and both edges of thigh, to proximal quarter (or less) of tail. Underneath whitish, except for following black markings in male: small patch on chin, spots on lower lips, chevron on throat (more angular than in nominate race, and with the junction of the arms tending to be prolonged forward, so that its shape is almost that of a tuning-fork), and large anchor-shaped patch on chest.

Upper labials 10-15. Line of 42-57 pores extending to knee, continuous or slightly broken and very slightly bowed forwards at midline. Gulars and ventrals smooth. Toes slightly compressed and denticulate. Lamellae under fourth toe 26-33, V-shaped in section sharply bicarinate, the inner series of keels apical, the outer series lateral and weaker. Maximum snout-vent length: males 67, females 65.

Distribution.—Sandplains of the south-western interior of Western Australia from Coorow south to Ongerup, and east to Boorabbin and Ravensthorpe.

Comments.—Specimens from the Coorow-Marchagee sandplain differ from typical *griseus* in their slightly keeled rather than smooth gulars and ventrals, indicating some relationship to the southern populations of nominate *maculatus*, which at Jurien Bay are only 60 miles to the west. Nevertheless, in their coloration and general proportions they hardly differ from typical *griseus*.

The known eastern limit of *griseus* in the north is at Boorabbin. Since the plant and soil formation it inhabits ceases about 50 miles east of Boorabbin, it is unlikely that its known range will be greatly extended in this latitude. In the south, however, suitable habitat extends eastward from Ravensthorpe (the present limit) to the Great Australian Bight. A small greyish *Amphibolurus* has been observed, but not collected, on bush tracks through dense mallee-heath south of Mt. Ragged. At Truslove (39 miles north of Esperance) I collected an adult female (R 17648) whose coloration is so different as to preclude its placing with *griseus*. This specimen has a snout-vent length of 52.5 mm. Dorsally it is pale grey. There is no dorsolateral stripe, and the unbroken and unconstricted blackish brown transverse bars are irregularly rectangular. Along the midline there is a series of short blackish brown dashes, and there are small spots of a similar colour between the transverse bars. It probably represents another race of *maculatus*, though in its proportions and structure it agrees with *griseus*.

***Amphibolurus maculatus dualis* subsp. nov.**

Holotype.—R 23637 (in Western Australian Museum), an adult male collected by G. M. Storr and A. M. Douglas on October 8, 1964.

Type locality.—7 miles south-southeast of Cocklebidy, Western Australia, in lat. 32° 08' S and long. 126° 08' E.

Paratypes.—R 23638-94 (7 mi. SSE of Cocklebidy).

Diagnosis.—Distinguished from all other races of *maculatus* by marked sexual differences in dorsal coloration. Males are very like those of *m. griseus*, but females are drab (generally dull brown with inconspicuous pattern).

Description.—Male dorsally brownish grey flecked with black on head and along midline of back and tail. Moderately broad dorsolateral stripe from neck to rump, orange-red, becoming pale posteriorly, continuous or narrowly

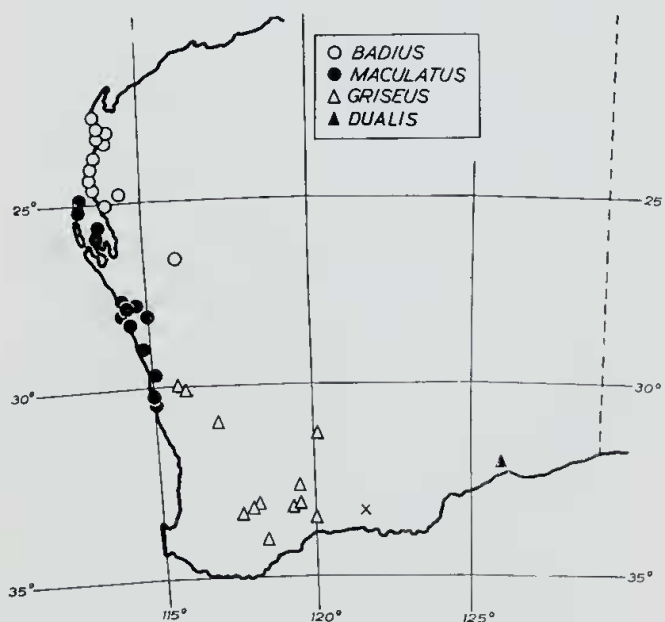


Fig. 1.—Location of specimens of four races of *Amphibolurus maculatus*. Cross indicates position of Truslove, where the peculiar R 17648 was collected.

broken with black. Dorsolateral stripe bordered above by series of blackish spots which usually coalesce to form a ragged-edged streak. Moderately broad greyish white lateral stripe from neck to anterior part of tail, interrupted at insertion of hindleg and obscurely present on both sides of thigh. Black ventrolateral stripe. Underneath whitish except for following black markings: on mental and adjacent scales, extending back as a broken or continuous stripe on lower lips; moderately broad chevron on anterior half of throat, continuous with or separate from narrow stripe extending back on to side of neck and anteroventral surface of arm; rhomboid patch on chest usually curved anteriorly and prolonged backwards on midline so that its resultant shape resembles anchor (when small) or silhouette of hawk (when large).

Female dorsally dull, slightly reddish, brown. Broad dorsolateral and lateral stripes, greyish white, narrowly edged with dark brown. On each side of dorsolateral stripe and below lateral stripe a series of dark brown spots, usually well spaced from each other but occasionally only separated by a few white dots. In most specimens some of the dark spots break dorsolateral stripe by obliquely and narrowly joining with their opposite number. In a few specimens the three series of brown spots align transversely to form broken bars. Tail narrowly and obscurely banded with white dots (probably homologous with those between dorsolateral dark spots). Underneath whitish except for more or less vague grey markings corresponding to black of males.

Upper labials 9-14. Line of 37-53 pores extending to (or almost to) knee, narrowly broken and slightly bowed forwards at midline. Gulars and ventrals smooth. Toes slightly compressed, denticulate along outer edge. Lamellae under fourth toe 24-30, sharply bicarinate, the outer series of keels slightly weaker. Maximum snout-vent length: males 57.5, females 59.

Distribution.—Only known from the type locality, which is in the narrow zone between the southern edge of the Nullarbor Plain and the Great Australian Bight.

Comments.—The above population was discovered after the submission of this paper for publication and I am grateful to the Hon. Editor for permission to describe it here.

These lizards were found in a small area of mallee-spinifex growing on shallow reddish loam over limestone. They constitute a partial exception to the generalisation (discussed later) that taxa inhabiting reddish soils have a reddish dorsum. The coloration of males is much the same as in *griseus*, but females are only a little less red than the substrate. It is possible that this race has evolved since the relatively recent colonisation by *griseus* of an arid, red-soil habitat, and that selection for harmony between coloration of dorsum and soil is much weaker in males than in gravid females.

***Amphibolurus fordi* sp. nov.**

Holotype.—R 19151 (in Western Australian Museum), an adult male collected by J. R. Ford on January 1, 1963.

Type locality.—12 miles north-west of Coolgardie, Western Australia, in lat. 30° 49' S and long. 121° 02' E.

Paratypes.—R 18663-70, R 19148-50 (12 mi. NW of Coolgardie); R 18671 (Comet Vale); R 17336 (18 mi. SSE of Karonie); R 12950 (12 mi. NW of Cundeelee); R 18672-3 (10 mi. E. of Zanthus).

Diagnosis.—Generally similar to *maculatus* but distinguished by fewer pores (which do not extend on to distal quarter of thigh), spotted throat of males, and narrow, unbroken, black-edged dorsolateral stripe.

Description.—Dorsally reddish brown, somewhat browner on head and greyer on tail. Head, back and tail (all or singly) may be finely spotted with black. Grey dorsolateral stripe from neck to rump, narrowly edged with black. Above and below dorsolateral stripe a line of black spots, the upper series terminating on rump, the lower series continuing on to tail where they coalesce to form black dorsolateral stripe. Grey lateral stripe, considerably broader than dorsolateral stripe, from axilla along flanks and both sides of thigh to middle of tail. Lateral stripe bordered below by black ventrolateral stripe from axilla to base to tail. Underneath whitish except for following black markings in males: spots or short bars on throat (sometimes so aligned as to suggest a chevron) and transverse bar on chest, narrowly prolonged on to forearm and often narrowly extended back on midline (in the latter event the resultant shape of the patch resembles the silhouette of a hawk).

Upper labials 12-16. Line of 34-42 pores extending three-quarters way down thigh, broken and slightly bowed forwards at midline. Gulars smooth. Ventrals weakly keeled and imbricate on chest, becoming smooth and juxtaposed on abdomen. Toes slightly compressed, their outer edge denticulate. Lamellae under fourth toe 28-34, obtusely V-shaped in section with a series of sharp keels along apex and one or more series of smaller keels along outer side of lamellae. Maximum snout-vent length: males 51.5, females 53.

Distribution.—Sandplains of the south-eastern interior of Western Australia from Comet Vale and Coolgardie east to the southern edge of the Great Victoria Desert.

Comments.—This species has been named after Mr. J. R. Ford, an Honorary Associate of this Museum, who collected the holotype and many of the paratypes.

An adult male (R 18694) from Boorabbie (150 miles north-east of Loongana) has been excluded from the type series. It is paler and has fewer pores (33) and more subdigital lamellae (35) than any of the paratypes. It may prove to belong to another race. Boorabbie is 300 miles ENE of Zanthus, the nearest locality of typical *fordi*.

The distribution of *fordi* is almost contiguous to that of *maculatus griseus*; yet the two taxa differ markedly: *fordi* is much the smaller, and being reddish in coloration, is superficially most like *badius* of the races of *maculatus*. Since gene-flow seems to have long ceased between these neighbouring taxa, *fordi* can hardly be

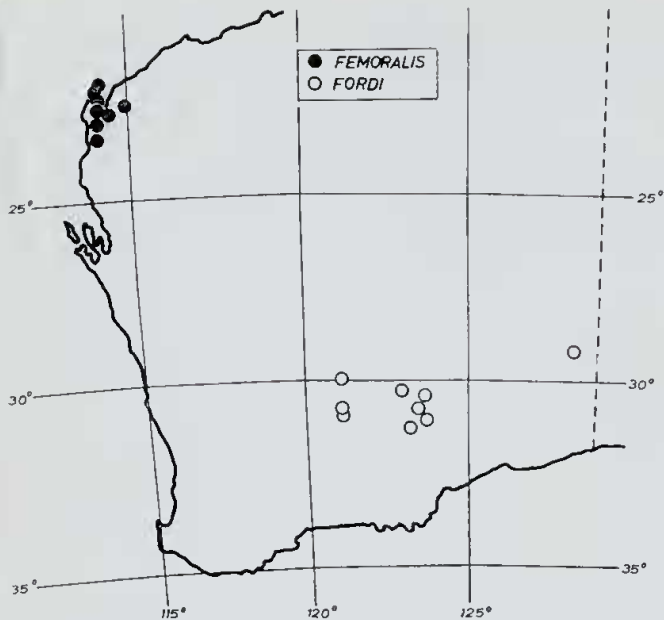


Fig. 2.—Location of specimens of *Amphibolurus femoralis* and *fordi*.

treated as another race of *maculatus*. Moreover, in certain respects, e.g. the reduction in femoral pores and of black on the throat of males, it is less like *maculatus* than the species about to be described.

***Amphibolurus femoralis* sp. nov.**

Holotype.—R 17008 (in Western Australian Museum), an adult male collected by G. M. Storr and B. T. Clay on October 19, 1962.

Type locality.—23 miles north-east of Giralia, Western Australia, in lat. 22° 29' S and long. 114° 33' E.

Paratypes.—R 9008 (Northwest Cape); R 18685 (5 mi. N of Learmonth); R 18683-4 (6 mi. S of Learmonth); R 18681-2 (13 mi. S of Exmouth Gulf HS.); R 17013-8 (9 mi. NE of Yanrey); R 18686-92 (9 mi. NE of Giralia); R 17100-4 (4 mi. W of Bullara); R 18678-80 (18 mi. SSW of Bullara); R 18674-6 (15 mi. SE of Cardabia).

Diagnosis.—Coloration much paler than in other members of this species-group and pattern more obscure. Pores less numerous and not extending beyond middle of thigh. Black ventral markings in male confined to chest.

Description.—Dorsally pale brick-red, finely dotted with brown. Narrow, discontinuous, grey dorsolateral stripe sometimes discernible between neck and rump. A more prominent pale lateral stripe from axilla to middle of tail, with an interruption at insertion of thigh. Above this a dark brown stripe on tail, which is represented on body by a slight clumping and darkening of dorsal spots. Vaguely defined strip of grey below lateral stripe. Underneath whitish except for black patch on chest of males that would be kite-shaped but for its narrow extension on to fore-arms.

Upper labials 11-15. Line of 18-32 inconspicuous pores scarcely extending to middle of thigh and broadly discontinuous at midline. Gulars smooth or weakly keeled. Ventrals weakly to moderately keeled. Toes long, slender and compressed, the outer margin of their upper

surface strongly denticulate. Lamellae under fourth toe 26-37, V-shaped in section, their apex bearing a series of sharp keels largest and highest on middle phalanges. Claws long and slender. Maximum snout-vent length: males 57, females 54.

Distribution.—The Exmouth Gulf region of Western Australia, from Northwest Cape and Yanrey south to the Tropic.

Comments.—Although *femoralis* has been represented in this Museum since 1946, its distinctiveness was not appreciated till A. Kluge found it sympatric with *Amphibolurus isolepis* in September, 1961. I am indebted to Mr. Kluge for pointing out its femoral characters and for the loan of his series of this and related species.

***Amphibolurus isolepis isolepis* (Fischer)**

Grammatophora isolepis Fischer, 1881, Arch. Naturgesch. 47: 232. Nickol Bay, Western Australia (F. von Mueller).

Material examined.—R 3447 (La Grange); R 1087-96 (Wallal); R 2117 (De Grey); R 14592-3 (Strelley); R 14594 (7 mi. SE of Port Hedland); R 17057-8 (Bocdarie); R 18745-79 (Mundabullangana); R 17068 (12 mi. E of Mundabullangana); R 17062-3 (15 mi. E of Mundabullangana); R 17078 (20 mi. SE of Mundabullangana); R 18780-5 (28 mi. SE of Mundabullangana); R 12625-8, R 13064-5, R 13314, R 18798-9 (Woodstock); R 20012-3 (7 mi E of Mt. Ulric); R 18795-7 (Millstream); R 18786-91 (Cossack); R 17022 (Nickol Bay); R 18792-4 (Karratha); R 14337, R 14349-54 (Legendre Island, Dampier Archipelago); R 5017-8 (Warrawagine); R 4022-6 (Canning Stock Route); R 3946, R 3957-8 (Well 35, Canning S. R.); R 4057 (Well 32, Canning S. R.); R 3932-4 (between Wells 31 and 36, Canning S. R.); R 3924-9 (Well 31, Canning S. R.) R 3916 (Well 30, Canning S. R.); R 3904-5 (Well 29, Canning S. R.); R 21453 (Tennant Creek, N.T.); R 13142-4 (Yardie Creek); Kluge 445-7 (5 mi. SW of Vlaming Head); R 18701-8 (2 mi. SW of Vlaming Head); R 21351 (Northwest Cape); Kluge 398, 402, 404-5 (6 mi. SE Vlaming Head); R 18709, Kluge 481 (10 mi. SE of Vlaming Head); R 18718-21 (4 mi. S of Learmonth); R 18710-6 (6 mi S of Learmonth); Kluge 362-3, 365, 370, 387-93 (7 mi SSW of Learmonth); Bradshaw collection (Learmonth and 4 mi. NW of Exmouth Gulf H. S.); R 18717 (12 mi. SW of Exmouth Gulf H. S.); R 16992-3 (16 mi. NE of Ningaloo); R 18718-21 (4 mi. S of Exmouth Gulf H. S.); R 18722-4 (13 mi. S of Exmouth Gulf H. S.); R 18699-700 (18 mi. SSW of Bullara); Kluge 346-53 (6 mi. N of Warroora).

Description.—Dorsally reddish brown, irregularly freckled with blackish brown and spotted with yellowish brown (spots of latter colour may be absent, or narrowly edged with dark brown so as to form ocelli). Pale, dark-edged dorsolateral stripe from occiput to tail, becoming increasingly broken and obscure posteriorly. A similar pale, dark-edged lateral stripe, from shoulder to groin, extends on to tail as a series of pale spots; in adult males it extends forward, above tympanum and through orbit and lores to snout. Between pale lateral and dorsolateral stripes, and also immediately above latter, a widely spaced series of dark brown spots, the first series tending to coalesce in males to form

a broad stripe. Lips yellow. Underneath whitish except in adult and subadult males which have a broad strip of jet black from snout to middle of abdomen, constricting at gular fold and dilating on chest. Adult males also have a dark stripe on anteroventral surface of arm which extends forward to posterior edge of tympanum; it may (but normally does not) continue forward from tympanum, as an increasingly narrow stripe between eye and lips, to about level of nostril. Anteroventral surface of hind-legs also black in fully adult males. Adult females may have male ventral pattern indicated by pale grey flecking, especially on throat.

Upper labials 10-13. Continuous line of 43-62 pores extending almost to knee and strongly arched forward at midline (pores much smaller in females but clearly discernible). Gulars keeled and imbricate, becoming very small towards gular fold. Ventrals largest on chest where they are strongly keeled and imbricate, becoming smaller and smoother on abdomen. Toes slightly compressed and weakly denticulate along their outer edge. Lamellae under fourth toe 25-35, V-shaped in section, weakly keeled apically (in some specimens, especially females, keels sharp and in two series). Claws moderately long. Maximum snout-vent length: males 68, females 70.

Distribution.—Arid and semiarid regions of tropical Western Australia from the southern parts of the Kimberley Division south-west to the Pilbara region and south-east into the Northern Territory, with an isolated population from Northwest Cape south to Warroora.

Comments.—In spite of its geographical separation (by the next race) from the main bloc of *i. isolepis*, the Northwest Cape population is not so distinctive as some others. The lizards inhabiting the alluvial plains of the middle Fortescue are very dark and, like those from nearby Woodstock, are rather larger than coastal animals.

Even more distinctive is the population inhabiting Legendre, a low calcareous island in the Dampier Archipelago. The dorsal coloration of the single adult (a male with snout-vent length of 52 mm) is quite bereft of red, and its tail is relatively longer than any other specimen of Pilbara *isolepis*. The rest of the series are juveniles ranging in snout-vent length from 24.5 to 38 (av. 29). They were collected in June, at which time on the mainland juveniles are considerably larger and adults have not been collected (see Table IV). This population is either smaller in size than those of the mainland or (more probably) breeds later. It may prove worthy of subspecific distinction.

Fischer gave the locality of *isolepis* merely as Western Australia. His description, however, was so detailed as to leave little doubt that it applied to Pilbara lizards. Dr. H. Wermuth (Staatliches Museum für Naturkunde, Stuttgart) has informed me (*in litt.*, 27/vii/64) that the types were collected at Nickol Bay in 1880. Dr. Wermuth has kindly lent me the types, an excellently preserved male and female with catalogue number 2051. They agree closely with our Pilbara mainland series. The tail of the syntype male is intact and relatively much shorter than in our Legendre Island male.

Amphibolurus isolepis rubens subsp. nov.

Holotype.—R 18740 (in Western Australian Museum), an adult male collected by G. M. Storr and B. T. Clay on November 3, 1961.

Type locality.—Yanrey, Western Australia, in lat. 22° 30' S and long. 114° 48' E.

Paratypes.—R 17019-20 (4 mi. E of Onslow); R 12624 (Koordarrie); R 17009-12 (9 mi. NE of Yanrey); R 18743-4 (14 mi. E of Yanrey); R 18741-2 (Yanrey); R 17004-7 (23 mi. NE of Giralia); R 18725 (9 mi. NE of Giralia); R 13125, R 13318 (176-mile Tank, 22 mi. NE of Winning); R 18736-9 (16 mi. NE of Winning); R 5331 (Marilia); R 5009 (Mia Mia); R 18695-8 (6 mi. SE of Gnaraloo); R 16953 (Yalobia).

Diagnosis.—By far the largest known race of *isolepis*. Juveniles and subadults similar in coloration to those of nominate race. Adults much paler, the assumption of a rosy flush, especially in males, almost completely masking dorsal and lateral colour pattern.

Description.—Adult male dorsally brownish pink, brownest on head and reddest on tail. Dorsal spots and dorsolateral stripe barely discernible. No black on side of head and body, except for spot anterior to oblique prolongation of gular fold. Ventral black more extensive and continuous than in other races of *isolepis*: it covers chin and throat (except for ventrolateral surface of jaw) and ventrolateral (and often ventral) surface of fore limb; broad patch on chest extends back on to abdomen (where it becomes narrow only towards pubis) and spreads broadly on to anteroventral and ventral surfaces of hind limbs, the black ceasing posteriorly along femoral pore line, though triangle between vent and preanal pores usually black. All ventral black continuous except occasionally for break on posterior of abdomen.

Adult female covered with pinkish flush, but not to same extent as in male, and much more of subadult pattern persists. Back covered with

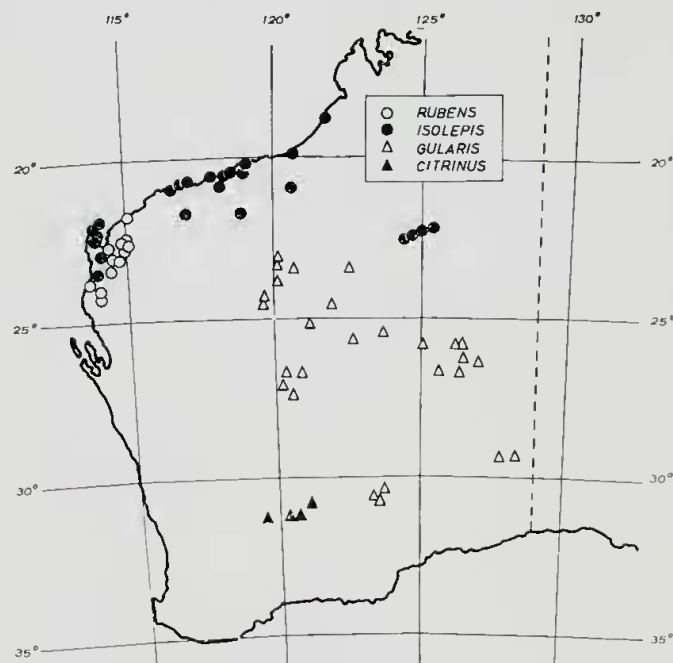


Fig. 3.—Location of specimens of four races of *Amphibolurus isolepis*.

brown spots, mixed with dark-edged pale spots (indiscernible on palest specimens). Brown spots not usually discernible on sides of body; they are represented on tail by brown stripe.

Upper labials 11-15. Continuous line of 53-70 pores extending to end of thigh and strongly arched forward at midline (pores much smaller in females but clearly discernible). Gulars imbricate and smooth or weakly keeled. Ventrals keeled, largest on chest. Toes slightly compressed, weakly to moderately denticulate along their outer edge. Lamellae under fourth toe 30-35, v-shaped in section, weakly to moderately keeled (usually in an apical series but occasionally with an additional smaller series on outer slope of lamellae). Maximum snout-vent length: Males 83, and females 77.5.

Distribution.—The Exmouth Gulf region of Western Australia from Onslow south to Gnarlaloo and Yalobia.

***Amphibolurus isolepis gularis* (Sternfeld)**

Amphibolurus maculatus gularis Sternfeld, 1924, Abh. Senck. Naturf. Ges. 38: 231. Hermannsburg, Northern Territory (M. von Leonhardi).

Material examined.—R 8421-3 (Lake Disappointment); R 13593, R 13599 (Jigalong); R 18800-3 (Ethel Creek HS.); R 18804 (25 mi. S of Ethel Creek HS.); R 18805-8 (Mundiwindi, new site); R 18809-11 (Ilgararri Creek); R 18812-9 (10 mi. S of Ilgararri Creek); R 18820-4 (20 mi. NE of Three Rivers HS.); R 15834-8 (17 mi. NE of Weld Spring, Canning S.R.); R 15854-5 (Pierre Spring, Canning S.R.); R 21113-4 (14 mi. E of Wiluna); R 21108-11 (35 mi. E of Wiluna); R 21074 (21 mi. W of Carnegie); R 21055-61 (58 mi. ENE of Carnegie); R 21028-9 (7 mi. NW of Lake Breaden); R 21026 (16 mi. E of Todd Range); R 14609-14 (40 mi. N of Warburton Range); R 14615, R 22041, R 22194 (Warburton Range); R 18227 (8 mi. W of Warburton Range); R 18828-9 (35 mi. E of Warburton Range); R 15712 (Featherstonehaugh Hill); R 15724 (Gahnda Rock-hole); R 19781-2 (Albion Downs); R 12409-11, R 18825-6 (Kathleen Valley); R 12948-53 (12 mi. NW of Cundeelee); R 21666-71 (5 mi. NW of Cundeelee); R 21684-8 (13 mi. NE of Cundeelee); R 13002-21, R 18860, R 21690-6 (Queen Victoria Spring); R 18861 (Iltoon, 125 mi. NNE of Loongana); R 18862-8 (Boorabbie, 150 mi. NE of Loongana).

Diagnosis.—Distinguished from nominate race mainly by colour and pattern. Dorsal coloration brighter, with greater development of ocelli. Dorsolateral stripe usually breaking up into pale, dark-edged spots. Much more black in adult males on side of body and head, with black of throat extending to edge of jaw.

Description.—Dorsal coloration orange brown to brick-red, finely spotted with black. Along each side of midline an irregular series of pale spots, narrowly edged with dark brown and sometimes coalescing to form short, rounded, transverse or longitudinal bars. Pale, dark-edged dorsolateral stripe from posterior edge of tympanum to proximal quarter of tail, usually broken behind shoulder to form a series of elongate spots. Above and below dorsolateral stripe a series of dark brown or black spots. Pale lateral stripe on flanks (similar in width and colour to dorsolateral stripe but seldom

broken) becoming ventrolateral as it extends irregularly forward to lips and backward on to tail. Pattern on flanks of males usually masked by broad strip of velvety black which, with decreasing width, extends forward across ear and above lips to tip of snout, and backward on to anteroventral surface of hind-leg. Lips yellow. Underneath whitish except in adult and subadult males which have throat, chest and anterior part of abdomen solid black (the same areas, especially throat, may be speckled with grey in gravid females).

Upper labials 10-16. Continuous line of 44-64 pores extending to end of thigh and strongly arched forward at midline. Gulars small and weakly keeled and imbricate. Ventrals larger and more strongly keeled, especially on breast where they are also mucronate. Toes slightly compressed and weakly denticulate along their outer edge. Lamellae under fourth toe 26-35, V-shaped in section and sharply keeled (one series of keels along apex, and one or two series on outer slope of proximal lamellae). Maximum snout-vent length: males 62, females 66.5.

Distribution.—The Gibson and Great Victoria Deserts of Western Australia, west to the sources of the Fortescue and Gascoyne Rivers, Wiluna and Queen Victoria Spring, and east into the southernmost part of the Northern Territory (and probably the north-west of South Australia).

Comments.—This race is excellently figured in colour by Lucas & Frost (1896).

Despite its enormous range, *gularis* undergoes little geographical variation. Northern specimens are redder and a little larger than those from the south. The dorsal coloration in the Cundeelee-Queen Victoria Spring population tends towards orange; it is only in this respect and its slightly smaller size that it approaches the next race.

***Amphibolurus isolepis eitrinus* subsp. nov.**

Holotype.—R21706 (in Western Australian Museum), an adult male collected by G. M. Storr on November 11, 1963.

Type locality.—2 miles west of Boorabbin, Western Australia, in lat. 31° 12' S and long. 120° 17' E.

Paratypes.—R 21710 (12 mi. E of Southern Cross), R 21707 (2 mi. W of Boorabbin); R 14121, R 14125 (Dedari); R 18830-7 (12 mi. NW of Coolgardie).

Diagnosis.—Distinguished from *gularis* by its yellow rather than reddish dorsal coloration. Also smaller and with relatively shorter tail and broader head.

Description.—Dorsally lemon-yellow with scattered spots of black (males) or dark brown (females) mixed with irregularly shaped, narrowly brown-edged, pale spots sometimes coalescing to form rounded transverse bars. Pale dorsolateral stripe, narrowly edged with brown, from nape to shoulder from which it continues as a series of pale spots similar to but larger than those along middle of back. Lateral stripe similarly broken into a series of dark-edged pale spots. Between lateral and dorsolateral series of pale spots a series of dark brown spots simi-

TABLE I

Mean length of head, etc. in males, expressed as per cent. length of trunk, and the ratio width to length of head, with female data in parentheses.

	Number of specimens	Percentage length of trunk				Ratio, width to length of head
		Head	Tail	Hind-leg	Fore-leg	
Femoralis	23 (11)	34 (34)	380 (351)	130 (126)	57 (57)	0.75 (0.77)
Fordi	13 (4)	37 (35)	327 (304)	124 (115)	57 (54)	0.77 (0.78)
Badius	26 (11)	37 (37)	357 (339)	116 (111)	56 (55)	0.73 (0.74)
Maculatus	17 (11)	36 (35)	362 (323)	117 (111)	56 (54)	0.76 (0.76)
Griseus	13 (9)	36 (35)	317 (301)	113 (107)	57 (55)	0.78 (0.78)
Dualis	22 (11)	38 (37)	323 (303)	121 (113)	57 (55)	0.77 (0.79)
Isolepis	58 (52)	39 (38)	328 (319)	123 (119)	57 (56)	0.74 (0.73)
Rubens	40 (19)	40 (36)	334 (324)	123 (119)	57 (56)	0.74 (0.74)
Gularis	75 (63)	39 (36)	317 (298)	129 (121)	58 (56)	0.75 (0.76)
Citrinus	6 (5)	39 (38)	279 (263)	119 (111)	58 (56)	0.80 (0.83)

lar to those on back. As in *gularis*, flank pattern masked in males by broad strip of velvety black which, decreasing in width, passes forward across ear and above lips to tip of snout, and backward on to anteroventral surface of hind-leg. Lips yellow. Underneath whitish except for broad velvety black patch on throat of males, continuous with large triangular patch on chest, its apex hardly reaching to abdomen and its base narrowly extending on to arm. Throat may be speckled in gravid females.

Upper labials 12-15. Continuous line of 50-58 pores extending to end of thigh and strongly arched forward at midline. Gulars juxtaposed or weakly imbricate, smooth or weakly keeled, becoming very small in vicinity of poorly developed gular fold. Ventrals large and keeled on chest, becoming smaller, juxtaposed and smooth on abdomen. Toes relatively short and stout, slightly or not compressed, weakly denticulate. Lamellae under fourth toe 24-34, U-shaped in section, weakly or moderately bicarinate, the outer series of keels usually becoming very small on distal phalanges and sometimes disappearing. Maximum snout-vent length: males 50, females 57.

Distribution.—Sandplains between Southern Cross and Coolgardie in the southern interior of Western Australia.

Comparative Mensuration and Meristics

The following measurements were made on all animals old enough to sex by coloration:—length and width of head, and length of tail, foreleg and hindleg (the last two measurements exclusive of claw). All these measurements, except width of head, were expressed as percentage length of trunk (snout-vent length minus length of head); the means of these and of the ratio width to length of head are given in Table I. The length of appendages relative to trunk and the ratio width to length of head all decrease with age. To illustrate one of these effects, Table II gives the relative length of hindleg for various size groups in two races of *isolepis*. Upper labials, subdigital lamellae and pores were counted in a substantial proportion of each sample; means and standard deviations are given in Table II (the number of pores are based solely on male counts).

All appendages are relatively shorter in females than males. The disparity is greatest in the tail (6%) and least in the foreleg (3%). The ratio width to length of head averages 1% greater in females than males.

The taxa within each species are tabulated in a north-south sequence, which reveals the tendency for relative length of appendages (except foreleg) to decrease from north to south, in accordance with Allen's rule. The ratio width to length of head increases from north to south. These trends operate within species and not between them. For example, the northernmost race (*badius*) of *maculatus* is shorter-legged than the southernmost race (*citrinus*) of *isolepis*. It so happens that *maculatus* is a short-legged (and long-tailed) species compared to *isolepis*. Differences in relative proportions are very pronounced between *femoralis* and *isolepis rubens*, even though their ranges are largely concurrent.

That the relative length of appendages within a race is a function of age rather than size is demonstrated in Table II. Overall mean relative length of hind-leg is almost identical in *i. isolepis* and *i. rubens*, but for any given snout-vent length the hindleg is considerably longer in the latter. Now *rubens* is a larger lizard than *isolepis*; hence individuals of the same size as *isolepis* would be younger.

Two more latitudinal trends are revealed in Table III, viz. increasing upper labials and decreasing subdigital lamellae from north to south. Lamellar counts in *m. badius* and *i. isolepis* are anomalously low.

Longevity

Of our large series of *i. isolepis*, the precise date of collection is known for 131 specimens. When these are classified chronologically, as in Table IV, it is seen that there is no overlapping of generations. Only juveniles have been collected in autumn; they grow throughout winter, mature rapidly in early spring, continue to grow after breeding, and die by the following

TABLE II

Mean length (mm) of hind-leg, expressed as per cent. length of trunk, for different size-groups of males in two races of *isolepis*, with number in sample in parentheses.

Snout—vent length	<i>i. rubens</i>	<i>i. isolepis</i>
80-84	110 (2)
75-79	118 (6)
70-74	121 (12)
65-69	126 (10)	117 (9)
60-64	129 (5)	120 (16)
55-59	131 (3)	121 (12)
50-54	127 (2)	130 (12)
45-49	131 (9)

autumn. In *i. gularis* the generations overlap in summer and autumn. Otherwise each sample consists of a single generation, the individuals of which vary considerably, but normally, in snout-vent length. In *m. maculatus* the generations overlap only in summer. But as all three taxa are poorly represented by summer and autumn samples, there could well be a general overlapping of generations from December to May, in which case the maximum age of the lizards would be about 18 months. Mean longevity is no doubt considerably less, and for all practical purposes these lizards may be deemed annual. The data for the other six taxa, though fragmentary, are not inconsistent with the above pattern.

Most of the large size-variation within generations is probably due to protraction of the breeding season. In summer 1961-2, females of *i. isolepis* contained large yolky eggs as early as November 2 and as late as March 4.

Habitat Preferences

The species *isolepis* occupies habitats that are generally characterised by great summer heat and low irregular rainfall. The race *citrinus* alone is found in an area where winter rains are fairly reliable. The remaining races, with the partial exception of the Cundeelee-Queen Victoria Spring population of *gularis* and the

North West Cape population of *isolepis*, occur where winter and spring are normally seasons of drought.

Generally *isolepis* favours light reddish soils sparsely vegetated with spinifex (*Triodia* spp.). There are some exceptions to this generalisation, notably the western population of *citrinus* which occurs on yellow sand covered with a fairly dense shrubbery of Myrtaceae and Proteaceae, and the dark mid-Fortescue population of *i. isolepis* which occurs on alluvial flats that support a dense sward of soft grasses after rain. Rocks are a rare feature in *isolepis* habitats. However, the nominate race may be found among granite boulders along the banks of the Maitland River at Karratha, and on sheets of limestone north-east of Ningaloo. The essential features of *isolepis* habitats (and indeed for all members of the species-group) are some bare ground on which to forage and take up heat, and some dense vegetation into which the lizards may scurry when hard-pressed, though normally they prefer, when chased, to run from one open space to another.

The various races of *maculatus*, even including *badius*, occur in areas where effective rain is largely confined to winter. The soils are usually sandy and, except in the north, not reddish. The prevailing vegetation is shrubby rather than grassy, and low trees may be plenti-

TABLE III

Mean (*M*) number of upper labials, lamellae under fourth toe, and pores, with sample size (*N*) and standard deviation (*S*).

	Upper labials			Subdigital lamellae			Pores		
	N*	M.	S.	N*	M.	S.	N.	M.	S.
Femoralis	62	12.8	1.1	59	32.0	2.5	19	24.4	3.0
Fordi	38	13.6	1.1	39	31.5	1.9	15	37.7	2.6
Badius	56	11.6	1.0	55	27.6	1.7	33	47.2	3.3
Maculatus	43	12.6	1.2	43	30.2	2.5	12	46.3	3.2
Griseus	43	12.8	1.0	42	29.0	1.8	9	45.0	4.2
Dualis	33	11.9	1.0	32	28.0	1.6	17	44.2	4.3
Isolepis	40	11.4	1.2	30	30.0	2.8	43	52.9	3.8
Rubens	19	12.5	1.0	19	33.0	1.6	32	60.7	3.7
Gularis	87	13.0	1.0	60	30.6	1.9	53	53.9	4.1
Citrinus	22	13.0	0.9	22	28.0	1.7	9	53.8	2.7

* The two sides of a single animal are counted as a sample of two.

TABLE IV

Range (*R*) in snout-vent length (mm) at different months of the year, with mean (*M*) and number (*N*) in samples (which have been partitioned into generations).

	i. isolepis			i. gularis			m. maculatus		
	N.	R.	M.	N.	R.	M.	N.	R.	M.
December	1	22	22	2	29-31	30.2
January	6	27-35	30.7	1	29	29
February
March	7	24-34	30.1
April	2	38-39	38.5
May	8	28-40	33.5	29	30-49	41.3
June	5	33-45	37.8
July	17	31-52	42.4	35	36-55	47.8
August	32	34-54	43.5	20	24-59	44.4
September	29	46-65	55.1	2	48	48	1	52	52
October	9	44-60	52.3	7	48-58	50.4
November	31	43-65	55.8	18	42-65	53.1
December	21	47-59	54.9	6	49-56	52.4
January	50	46-66	54.9	10	48-59	52.4
February	11	55-65	60.0
March	6	62-70	66.9	25	50-63	56.3
April	6	58-66	62.6
May	1	61	61

ful. In the few places where *maculatus* and *isolepis* are sympatric, as at North West Cape and east of Southern Cross, no differences are evident in habitat preferences.

Amphibolurus fordi occupies an area in which scanty rains are received in summer as well as winter. It is confined to isolated patches of red sand clothed with small spinifex and scattered mallee, a habitat it shares with the southernmost populations of *i. gularis*.

Although its geographical range is small, *femoralis* occurs in a variety of habitats. North-east of Giralda it is restricted to the almost bare tops of red sand dunes, whereas the much larger *i. rubens* monopolises the spinifex-covered interdunes. A little further west, beyond the range of *rubens*, *femoralis* is sympatric with *i. isolepis* and *m. badius*. It has been found with both of these on heavy loam vegetated with spinifex. It has also been found with *isolepis* on stony, clayey soils, and with *badius* on red dunes clothed with proteaceous shrubbery.

Phylogeny

The common feature in the colour pattern of the various members of this species-group are the pale lateral and dorsolateral stripes, which are otherwise rare in *Amphibolurus*. However a pale dorsolateral stripe occurs in *Physignathus*, *Diporiphora* and *Tympanocryptis*. Strongly keeled dorsal scales are also shared by members of these genera with the *maculatus* group. In their dorsal colour pattern these genera tend to combine pale longitudinal stripes with dark transverse bands, as in *Tympanocryptis lineata* and *Diporiphora* spp. Among the *maculatus* group this kind of pattern is best preserved in *maculatus* itself, where the break in the transverse bars may represent a former vertebral stripe now submerged in the dorsal ground coloration.

Despite their bright colours and bold patterns, all members of the species-group are inconspicuous against their natural background. The general coloration matches well with the substrate. All but three taxa occur on reddish soils, and all except these three are dorsally reddish. The pattern too is responsive to the environment. The transverse bars of *maculatus* are useful in habitats where the vegetation is high and dense enough to throw numerous shadows. But on the bare sunlit ground of arid habitats, barring would undoubtedly be disadvantageous. Furthermore, in arid habitats the dorsolateral stripe has undergone some modification. In *femoralis* and *i. rubens* it has almost disappeared; while in *i. gularis* and, to a lesser extent, *i. isolepis* it tends to break up into ocelli similar to those on the back.

While it is not unlikely that *maculatus* is the most primitive member of the group in colour pattern, it is not at all certain that it is primitive in other characters. With respect to number of pores and extent of ventral black in males, *femoralis*, *fordi*, *maculatus* and *isolepis* form a series. Whether the series has been formed by reduction, addition or both, there seems to be no way of ascertaining.

Regarding pores, I favour the hypothesis of reduction. Successive loss of preanal pores from near the midline would reduce the strong arch

of *isolepis* to the slight bow of *maculatus* and *fordi* and the straight alignment of *femoralis*. Such a sequence demands the loss of pores (a common event in the Agamidae) rather than the evolution in *isolepis* of a unique alignment of preanal pores.

The extent of ventral black is roughly correlated with body size. *I. citrinus* is clearly derived from *i. gularis*; it is considerably smaller than its parent race and has less ventral black. Conversely *i. rubens* is much larger than its presumed parent, *i. isolepis*, and has much more ventral black. In the series *m. griseus*, *m. maculatus* and *m. badius*, decreasing size is accompanied by decreasing ventral black. Within a taxon the ventral black (first attained by males when their snout-vent length is between 40 and 50 mm) continues to spread with growth, even after breeding. Hence change in the number of pores and relative extent of ventral black could be consequent of phylogenetic change in body-size.

Body-size is not consistently influenced by non-biotic factors such as latitude. Whereas *maculatus* increases in size from north to south, the opposite obtains in the sequence *isolepis-gularis-citrinus*. On the other hand the prior presence in a habitat of another member of the group could well determine whether an invader would advantageously increase or decrease its body size. With a snout-vent length of up to 67 mm, *griseus* is by far the largest race of *maculatus*, which is otherwise a smaller species than *isolepis*. East of Southern Cross *griseus* coexists with *citrinus* (SVL up to 57), the smallest race of *isolepis*. In the sandhill country east of Exmouth Gulf, *rubens* (SVL up to 83 and much the largest race of *isolepis*) coexists with *femoralis* (SVL up to 57).

Over most of the State the *maculatus* group is represented by only one species—*isolepis* in the north-east, and *maculatus* in the south-west. It is probable that the greater part of the evolution of the taxa has been allopatric, and that their morphological divergence has been acquired during their adaptation to the physical environment. More or less recently, certain taxa have expanded their range and have locally become sympatric with other members of the group. The taxa geographically intermediate between *maculatus* and *isolepis*, viz. *femoralis* and *fordi*, are especially exposed to competition. It is possible that each of these has independently undergone selection for sexual precocity, and that their reduction in pores and ventral black are concomitants of this precocity.

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